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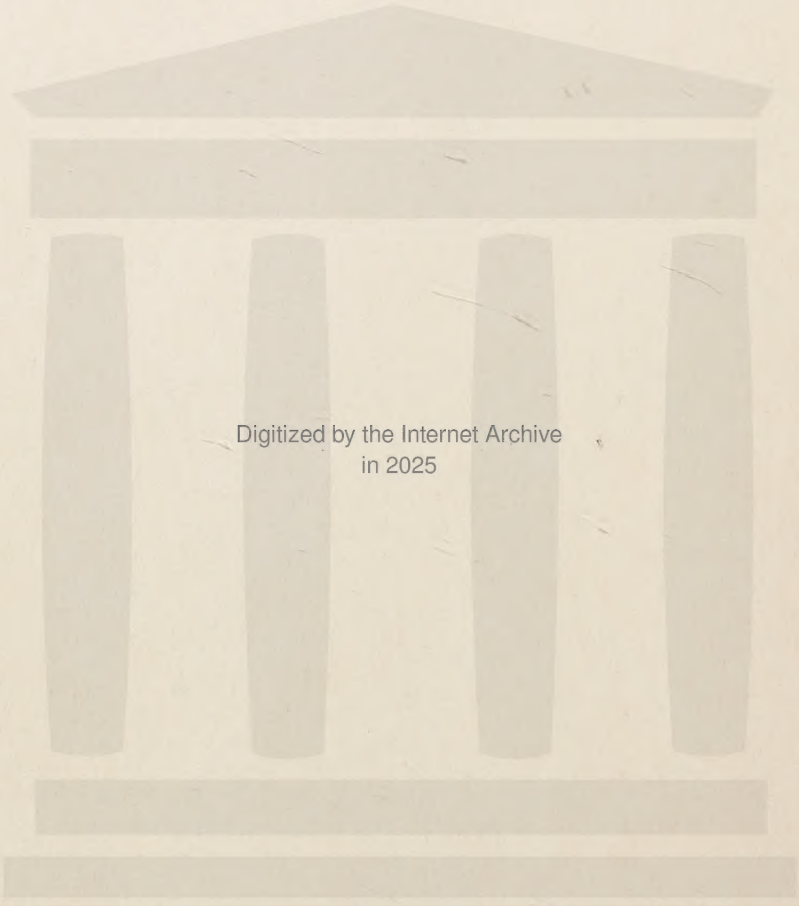

SELECTING AND BREEDING POTATOES FOR FIELD RESISTANCE TO VERTICILLIUM WILT IN IDAHO

JOHN G. MCLEAN[1]

THE WILT affecting Russet Burbank potatoes *(Solanum tuberosum L.)* in Idaho was described in 1948 by Nielsen (7)[2] as being due to *Verticillum albo-atrum* Reinke and Berth. In 1949, a cooperative potato-breeding project was initiated by the University of Idaho and the United States Department of Agriculture, the chief purpose of which was to incorporate resistance to Verticillium wilt into the russet-type potatoes.

Potatoes in the major producing area in eastern Idaho are generally affected by this disease. It has been estimated that throughout the area, 20 percent of the potential yield is lost with losses as high as 50 percent in some locations. The disease causes serious damage or early death of the susceptible plants in late August or early September, when the shorter days and cooler temperatures of late summer (Figure 1) provide the conditions which are most favorable for a maximum yield (9).

To evaluate the resistance or susceptibility of the numerous lines of potatoes available for testing, studies were made at the University of Idaho Branch Experiment Station at Aberdeen, Idaho, and on land donated by C. L. Parkinson, northwest of Rexburg, Idaho, on the Egin Bench. At Aberdeen, the tests were conducted on loam following crops of grain, alfalfa or potatoes to which 250 lbs. per acre of 16-20-0 fertilizer had been added. Plantings were made in early May and furrow irrigations were applied early in the growing season. The potatoes at Rexburg were grown on a sandy soil under conditions of sub-irrigation where the water level was maintained approximately 30 inches below the surface throughout the growing season. These tests were made on fields which had been planted to potatoes for the previous 1 or 2 years and received no supplemental fertilizer at planting.

SYMPTOMS

In 1948, the symptoms of Verticillium wilt in Idaho were described by Nielsen (7) as follows: "Chlorosis and wilting usually start in the basal leaves on one side of the plant and progress upward. In time most lower leaves wilt and die." The

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[2] Numbers in parenthesis refer to literature cited.

term "wilt" is confusing in that it may indicate wilting of the plant. This is not the case with many varieties. While some varieties show a rapid wilting of the stem, others may remain erect even after most of the leaves are dead and dry. The only indication of the disease in some varieties may be a few yellow leaves in one side of the plant and further symptoms may not develop for 15 to 30 days. Such plants are not seriously affected by the disease.

Symptoms produced by infection with *Verticillium albo-atrum* can readily be confused with those produced by *Fusarium oxysporum*, which produces yellowing and death of the lower leaves; with those of bacterial ring-rot, which is manifested by

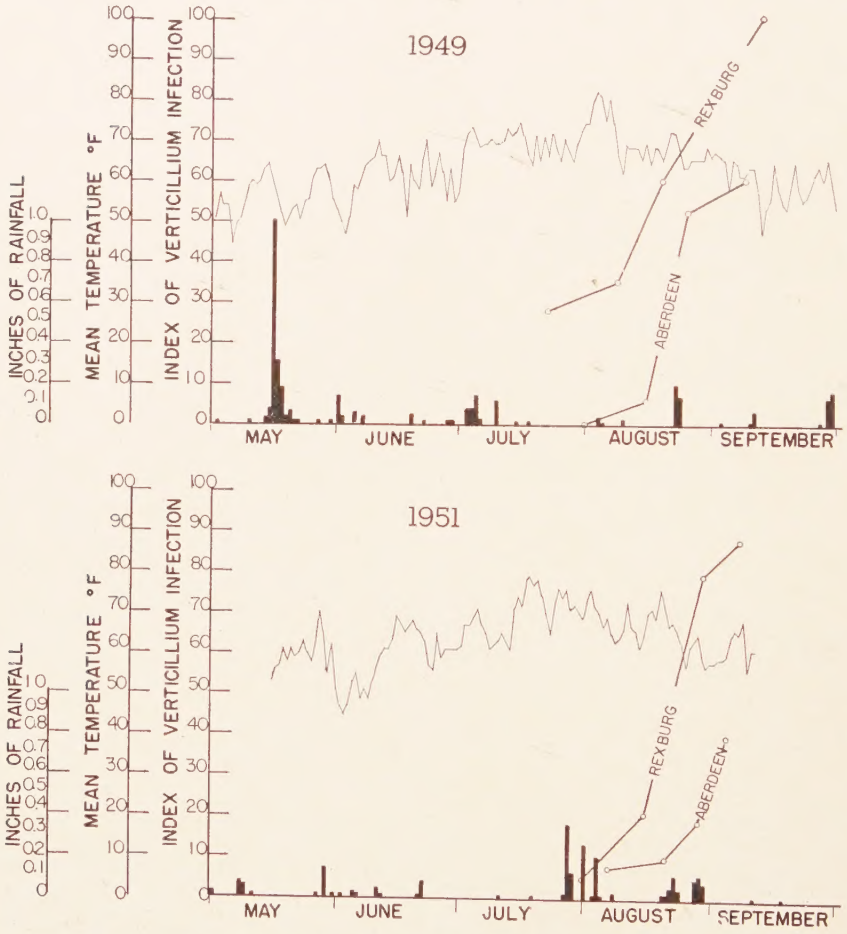

Figure 1. — A comparison of the mean daily temperatures and rainfall at Aberdeen, Idaho, and symptom development at Aberdeen and Rexburg in 1949 and 1951.

stem wilting and leaf burning; with the symptoms of late blight under dry conditions; or even with current-season symptoms caused by the leafroll virus. Late in the season, many varieties may show upward rolling of the apical leaflets, slight to marked pigmentation, and basal yellowing of the leaflets similar to the symptoms of leafroll. Examination of the lower stem in such plants, however, showed vascular discoloration associated with Verticillium infection. Upon replanting the tubers, a proportionate amount of leafroll was not found in the subsequent crop as would have been the case had leafroll caused the symptoms.

The tuber symptoms of Verticillium wilt are generally those discussed by Nielsen, who found vascular browning of the stem end usually not more than ¼ inch in extent. Exceptions may be found in Kennebec and other varieties where the brown color may extend several inches into the tuber. The tuber symptoms, "internal discoloration and cavities and pink eyes", as described and illustrated by Folsom (4) in Maine, are not genearlly associated with Verticillium wilt in Idaho.

DISEASE INDEX

It was apparent that the percentage of plants showing symptoms did not in itself adequately measure the effect of the disease on the plant or the yield, because the time of infection, the rapidity of disease advancement and time of death in relation to maturity were not considered in percentage readings. In addition, certain lines might become 100 percent infected late in the growing season without the yield being materially affected. For this reason, an index[3] of Verticillium infection was established. This was similar to the index used by McLean and Walker (6) to evaluate Fusarium wilt symptoms in potatoes. Arbitrary class weights ranging from 10 for slight infection to 100 for dead plants were set up to represent the effect of the disease. Symptom readings were made at 10-day intervals after the disease appeared. To give the time and severity of symptom expression and the rate of disease development, the last three readings of each season were averaged. This gave one figure, the *average Verticillium index* which could be used for comparison within a given maturity group to determine the relative resistance of each line. Comparisons could also be made in this way between years and locations and with known resistant or susceptible lines.

DISEASE DEVELOPMENT

Nielsen (7) reported that early planting increased the incidence and severity of Verticillium wilt on the Russet Burbank variety. It was generally observed that potatoes in earlier planted fields were affected earlier and more severely than were later

[3] Class weights were ascribed as follows: Slight—10, moderate—30, severe—50, and dead—100. Calculations were made on the basis of—

$$\frac{\text{total weighted values}}{\text{total number}} = \text{disease index}$$

plantings. Early irrigation appeared to have a similar hastening effect on disease development, as reported by Corey and Myers (2).

Nielsen (7) mentioned that high temperatures early in the growing season promoted the early appearance of symptoms. This can be seen in Table 1, where the accumulated degree-days[4] above a 50° F. mean can be inversely correlated with the time of first symptom expression. In 1949 and 1952, 270 and 295 such units had accumulated by June 10 while only 155 and 150 units were found during the same period in 1950 and 1951. The same relation between years held through June, with an approximate delay of 14 days in symptom expression with 100 less degree-day units by June 30 in 1950 and in 1951.

Table 1.—Relation of accumulated degree-days above a mean of 50° F. to the time of symptom appearance at Aberdeen, Idaho, 1949 to 1952.

Year	Accumulated degree-days					Days to symptom expression
	May 11-20	May 21-31	June 1-10	June 11-20	June 21-20	
1949	80	180	270	380	490	75
1950	30	95	155	265	395	86
1951	30	140	150	280	380	85
1952	50	125	295	315	495	68

Nielsen also pointed out that high summer temperatures increased the rate of disease development. The same results are shown in Figures 1 and 2. Parallel lines are observed in Figure

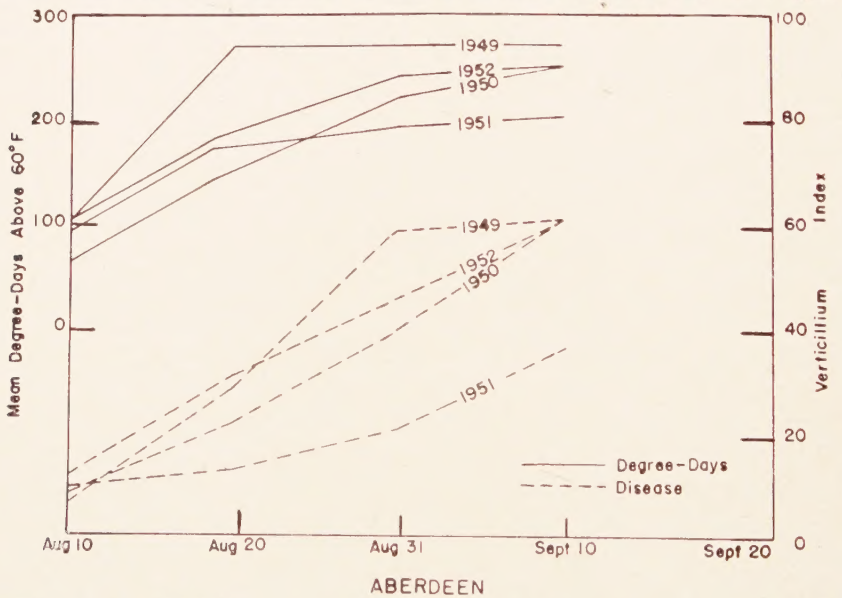

Figure 2.—Effect of accumulated degree-days above a 60° F. mean upon the increase and severity of disease symptoms at Aberdeen.

[4] Degree-days is a measure of heat units above a specified mean daily air temperature. If the daily mean was 53° F. this would produce three degree-days; 65° would be 15 degree-days.

2 which correlates the temperatures and symptom development at Aberdeen between August 10 and September 10. There is a 10-day lag between the rise in the temperature and the rise in the symptom development line. This can be most clearly seen in 1949. The lower level of infection throughout 1951 correlated with lower temperatures after August 10. There was an increase in severity of symptoms after August 31 with very little increase in accumulated temperatures. This increase could be attributed to the development of more severe symptoms in the plants which were already seriously affected and continued to decline even during cooler weather.

The daily mean temperatures, rainfall and disease development for 1949 and 1951 are compared in Figure 1. On August 15, 1949, disease development was less at Aberdeen than on August 15, 1951, despite the earlier appearance of the disease in 1949. The increase in symptoms between August 15 and August 25, 1949 was much greater than that in 1951. This followed the period of high temperatures in late July and early August while in 1951 the same period was characterized by decreasing temperatures and frequent showers and was followed by a very slow rise in the severity of the disease at Aberdeen.

The correlation between temperatures and disease increase at Rexburg is not as marked as at Aberdeen. This condition at Rexburg could be attributed to the more uniform and severe early infection from which the plants did not recover but got progressively worse, so that with cooler temperatures the disease was not delayed.

EFFECT OF MATURITY ON DISEASE DEVELOPMENT

The method used for reading the disease naturally produced a bias in favor of the late-maturing strains of potato. The early varieties received a high index reading because of the early and severe infection found in the field (Table 2). While considerable variation was found in the range for each group, a consistent trend appeared in the averages. The 3-year average index at Aberdeen ranged from 40.9 in the early varieties to 5.6 in the very late varieties and from 64.7 to 13.0 at Rexburg. Most of the varieties were tested for 2 of the 3 years at both locations.

In connection with the simulated hail-injury work of Takatori, Sparks, and Woodbury (8) at Aberdeen, it was noticed that plants which had been previously injured by the removal of leaves and were growing actively late in the season showed no symptoms of Verticillium wilt. The control plants, however, grown under identical conditions but with no leaf damage, were severely affected by the disease.

In a paper presented by T. H. Hankins at the annual meeting of the American Potato Association in 1947, it was indicated that the age of the tubers at planting time influenced the yield.

He proposed that 180 days from planting-to-planting was the optimum age for White Rose seed potatoes when replanted in February at Shafter, California. A yield reduction of approximately 100 lbs. per acre per day was realized when older seed stock was used.

Table 2.—Verticillium index readings of potatoes in various maturity groups at Aberdeen and Rexburg, Idaho, 1949 to 1951.

Maturity group	Index at Aberdeen[1]				Index at Rexburg[2]			
	1949	1950	1951	Average 3 years	1949	1950	1951	Average 3 years
Early	37.0	38.9	46.9	40.9	49.2	73.2	71.7	64.7
Early-medium	32.5	32.5	30.2	31.7	27.3	55.9	26.7	36.6
Medium	19.5	22.5	19.9	20.6	30.7	53.9	30.5	38.4
Medium-late	15.0	15.2	11.7	14.0	33.5	52.9	32.1	39.5
Late	7.2	16.6	6.6	10.1	19.6	36.9	14.1	23.5
Very late	4.9	6.7	5.3	5.6	7.3	22.1	9.7	13.0
Average	19.4	21.8	20.1		27.9	49.2	30.8	

[1] 114 named varieties.
[2] 93 named varieties.

It had been observed that early planting, early irrigation and early accumulation of heat units hastened maturity, and thus the development of the disease and also that early varieties were more rapidly and severely affected than late ones. Yarwood (10) and Nielsen (7) both reported that the later maturing strains of Russet Burbank were more resistant to Verticillium wilt than the common strain of the variety in California and Idaho.

In 1952, a preliminary test was initiated at Aberdeen to determine whether age of seed tubers of the same variety might affect the time of appearance and severity of the disease. Different aged tubers of 3 varieties were planted in early May. The immature seed stock had been treated with ethylene chlorohydrin to break dormancy. The results of this trial are shown in Table 3. The age of seed tubers, as referred to in the text and tables is considered as the length of time from planting to planting of the tubers. The normal age of tubers in Idaho was considered to be 12-month-old seed, with the 9-month, 7-month and 6-month-old seed being younger than normal.

Table 3.—Effect of age of seed tubers on time and severity of Verticillium symptoms at Aberdeen, Idaho in 1952.

Variety and source	Age of Seed tubers	Date of First symptoms	Maximum index Reading	Average index
	Months[1]			
Russet Burbank:				
Aberdeen, Idaho	12	July 15	60.0	39.3
Santa Maria, California	9	Aug. 11	30.0	20.3
Oceanside, California	7	Sept. 1	4.0	1.3
Greenhouse in Idaho	6	Sept. 1	2.0	0.7
White Rose:				
Aberdeen, Idaho	12	July 23	50.0	38.3
Porterville, California	7	Aug. 11	30.0	20.0
Early Gem:				
Aberdeen, Idaho	12	July 1	100.0	70.0
Greenhouse in Idaho	6	———	0.0	0.0

[1] Indicates age of seed from planting to planting.

Disease development in the 12-month-old tubers was normal for the growing season. In the Russet Burbank variety, symptoms appeared July 15 and the maximum reading was 60.0 and the average index 39.3; 9-month-old tubers produced plants which were later in showing symptoms and gave a lower disease reading, while with the 7-month and 6-month-old seed tubers the appearance of symptoms was delayed about 1½ months and the maximum and average disease readings were reduced from all of the plants showing severe damage to a few of the plants showing slight infection. A similar but less pronounced trend was found with White Rose. In Early Gem, however, no symptoms appeared during the growing season on plants from the 6-month seed tubers while plants grown from the older seed showed symptoms by July 1 and were dead before frost. The Early Gem plants from the young seed tubers were very late emerging and had just reached the blossom stage at the end of the growing season. No appreciable differences in yield were observed between the crops from the various seed sources of Russet Burbank or White Rose. Plants from the 6-month-old tubers of Early Gem, of course, produced no marketable tubers.

In 1953, at Rexburg, a similar trial was made with 4 susceptible varieties and 2 resistant ones with 12-month-old seed tubers grown in the field and 6-month-old seed tubers grown in the greenhouse. They were planted in duplicate lots of 5 hills each in mid-May after treatment with ethylene chlorohydrin. In the susceptible varieties Russet Burbank, Early Gem, Kennebec and Green Mountain, the symptom expression was delayed by approximately 20 days and the average index reduced by 20 or more units by the use of the younger tubers for seed, (Table 4). The resistant varieties, 41956 and Menominee, did not show early or severe symptoms so that the greatest difference between the ages of seed was only an index of 7.

Table 4.—Effect of age of seed tubers on Verticillium symptoms and the yield at Rexburg, Idaho, 1953.

Variety	Age of seed tubers	Verticillium index on 8/6	8/20	8/28	9/2	Average of 4 readings	Yield of 5 hills
	Months[1]						lbs.
Russet Burbank	12	2.0	8.0	45.0	50.0	26.3	6.5
Russet Burbank	6	.0	.0	5.0	5.0	2.5	9.5
Early Gem	12	6.0	18.0	42.0	65.0	32.8	8.7
Early Gem	6	.0	.0	.0	.0	.0	4.6
Kennebec	12	.0	27.0	63.0	73.0	40.8	7.2
Kennebec	6	.0	1.0	10.0	20.0	7.8	5.3
Green Mountain	12	5.0	32.0	40.0	70.0	36.8	8.2
Green Mountain	6	.0	.0	5.0	10.0	3.8	9.5
Menominee	12	.0	.0	.0	7.0	1.8	10.0
Menominee	6	.0	.0	.0	.0	.0	3.1
41956	12	.0	.0	.0	5.0	1.3	12.6
41956	6	.0	.0	.0	.0	.0	9.1

[1] Indicates age of seed from planting to planting.

A considerable increase in yield of Russet Burbank and Green Mountain potatoes was realized from the use of young tubers for seed, from 6.5 to 9.5 lbs. per 5 hills for Russet Burbank and from

8.2 to 9.5 lbs. for Green Mountain. The yields from the younger tubers of the two other susceptible varieties, Early Gem and Kennebec, both of which were late in emerging and were very immature at frost, were lower. Emergence from the 6-month-old seed stock of Menominee also was late and there was a correspondingly low yield. No appreciable difference could be seen between the different aged seed of 41956 during the growing season. The older tubers of this resistant variety, however, produced the greater yield, in contrast to the susceptible Russet Burbank and Green Mountain.

The delay in disease development produced by the use of young seed tubers of Russet Burbank and Green Mountain varieties made it possible to increase the yields so that they approached those of the resistant varieties.

EFFECT OF VERTICILLIUM WILT ON YIELD

At Aberdeen, the uniform infection by Verticillium was believed to reduce the yield of Russet Burbank potatoes by about 20 percent. It was not always possible to obtain a correlation between the disease index values and yield reduction under these conditions. On the Egin Bench, however, where the symptoms generally appeared earlier and advanced more rapidly, it was believed that more than 50 percent of the potential yield was lost from the disease. It was possible to obtain a high correlation between resistance and yield at Rexburg, which indicated that Verticillium wilt was a limiting factor in potato production. The results of 2-year variety tests are shown in Table 5.

Negative correlations between disease indexes and the total yields were highly significant for both years. In 1950, the correlation coefficient was -0.835 and in 1952 -0.889. The yields in

Table 5.—Effect of Verticillium wilt on yield at Rexburg, Idaho, 1950 and 1952.

1950			1952			
Variety	Verticillium index	Yield, sacks per acre	Variety	Verticillium index	Yield, sacks per acre	Yield U.S. No. 1, sacks per acre
Sequoia	7.1	553.6	Sequoia	3.2	401.6	377.5
A.C. 25669	5.3	504.6	A.C. 25669	12.6	386.2	306.6
Cayuga	36.1	468.3	Cayuga	21.9	262.5	172.2
A.C. 25671	13.0	462.8	A.C. 25671	38.4	273.0	238.6
Menominee	6.3	439.2	Menominee	8.5	342.1	305.2
White Rose	49.7	402.9	Furore	10.7	356.3	249.4
Saranac	1.8	363.0	41956	10.6	331.1	217.8
Green Mountain	45.0	332.0	Empire	12.5	269.8	260.1
Craigs Bounty	34.0	319.4	Craigs Bounty	6.8	324.7	295.5
Mohawk	36.1	312.2	Mohawk	27.9	238.7	214.8
Pontiac	58.7	304.9				
Record	28.3	268.6				
Irish Cobbler	70.5	252.3				
La Salle	55.0	245.0				
Progress	74.0	232.1				
Houma	73.0	197.8				
Russet Burbank	75.0	196.0	Russet Burbank	63.8	183.8	91.5
Red Warba	69.0	163.4	Red Warba	88.3	140.7	49.2
Least significant difference at 5% level	18.3	138.7		23.4	92.8	99.8

1950 ranged from 553.6 sacks per acre for Sequoia to 163.4 sacks per acre for Red Warba with corresponding disease values of 7.1 for the former and 69.0 for the latter. Several discrepancies could be noted in the trends of decreasing yield with increasing disease. Saranac, for example, which showed the least disease, produced 105 sacks per acre less than did Cayuga with a moderate disease reading. It was believed that Saranac, while highly resistant, required too long a growing season to mature a maximum yield of tubers. White Rose, with a relatively high disease reading, produced over 400 sacks per acre. Varieties such as White Rose showed increasing symptoms for a long period previous to death of the plant. Such varieties are not as seriously affected as are Russet Burbank, Irish Cobbler and Red Warba in which the symptoms advance more rapidly and result in early death to the infected plants.

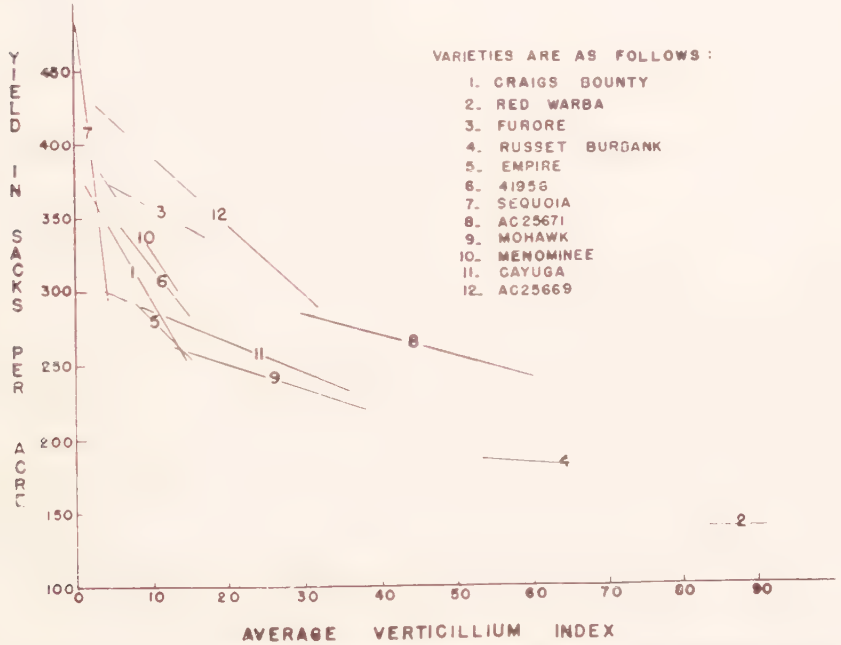

Figure 3.—The effects of Verticillium wilt on yield as shown by the varietal regression lines at Rexburg, Idaho, 1952.

The 18 varieties used in 1950 represent several levels of resistance while in 1952 some of the more resistant varieties are compared with 2 very susceptible varieties, Russet Burbank and Red Warba. The 1952 results are also shown graphically in Figure 3, which shows the regression line for each variety as calculated from the covariance analysis. A difference in yield of 260 sacks per acre was realized between the resistant Sequoia and the susceptible Red Warba variety. Despite the highly sig-

A. Menominee	Red Warba	Furore
Sequoia	A.C. 25671	Mohawk
Mohawk	Sequoia	Cayuga
Russet Burbank	A.C. 25669	41956

B. Russet Burbank	Empire	41956
Craigs Bounty	Cayuga	A.C. 25669
Empire	Furore	Craigs Bounty
Menominee	A.C. 25671	Red Warba

Figure 4.—Potato variety trial at Rexburg, Idaho, 1952. Russet Burbank is in left foreground of A. Red Warba is in right foreground of B.

nificant correlation values obtained, complete agreement between yield and disease was not always found. When the yield of U.S. No. 1 tubers was considered, however, the effects of the disease on producing small, unmarketable potatoes could be seen with Cayuga. The effects of severe infection on the size of tubers was especially marked in Russet Burbank and Red Warba, of which the marketable tubers were half or less of the total yield.

In Figure 4 A and B are shown two replications of the 1952 variety trial at Rexburg, which illustrate the differences in tuber size and yields between the various varieties. Differences between lots are not always apparent in the photograph, in which four 10-hill plots are represented in each row. In the left foreground of Figure 4 A, Russet Burbank, and the right foreground of Figure 4 B, Red Warba, the lower yield and smaller tubers of these wilt-susceptible varieties are readily apparent in comparison with those of the more resistant varieties adjacent to them. It is also interesting that 41956, not generally considered a high-yielding variety, produced a satisfactory yield of No. 1 tubers under these conditions.

VARIETAL RESISTANCE

During the 4-year period, 1949 to 1952 inclusive, approximately 1200 varieties and numbered seedlings were tested at Aberdeen for resistance to Verticillium wilt. The more promising lots were tested one or more years at Rexburg under conditions of severe disease development. When an analysis of variance was calculated on 90 lines of potatoes at 2 locations for 2 years on 3 maturity groups (early, medium, and late), highly significant differences were found between locations, years, and groups. While different index values were obtained for a single variety in different years, the classification of the variety as to resistance or susceptibility was usually the same. Infrequent discrepancies were generally found to be due to local soil conditions.

The disease readings at Rexburg were generally higher than at Aberdeen, as shown in Table 6, although the magnitude of differences between the two locations was not always consistent. Varieties such as Hindenburg, Ontario, and Yampa appeared to be somewhat resistant when tested at Aberdeen, but were moderately to seriously affected at Rexburg. Certain varieties were very susceptible, moderately susceptible or resistant at both locations.

Several different types of resistance were found in the many varieties. In varieties similar to Russet Rural, the late maturity of the strain was sufficient to make it appear resistant. In 1950, however, when the growing season was prolonged and disease readings could be made as late as September 27, the Russet Rural variety was seriously affected by mid-September. Many such varieties, even though susceptible, were able to produce an ade-

Table 6.—Average disease readings on named or numbered varieties at Aberdeen and Rexburg, Idaho.

Variety	Aberdeen		Rexburg	
	Average Verticillium index	Number of years tested	Average Verticillium index	Number of years tested
x 1276-185	51.9	4	52.4	2
41956	1.6	3	8.0	4
46952	52.0	4	65.3	3
A.C. 25669	8.0	3	5.0	4
A.C. 25671	8.6	4	29.5	3
A.C. 25673	3.0	2	0.8	2
A.C. 25680	1.7	4	2.1	2
A.C. 25682	25.8	2	83.3	2
Albion	12.5	2	47.7	2
Arnica	6.7	2		
Ackersegen	6.0	2		
Ashworth	37.0	1		
Aussie 96	5.1	4	6.7	3
Aquila No. 5	4.0	4	6.1	3
Cayuga	16.8	4	26.4	3
Chenango	13.3	1		
Chippewa	6.5	3	30.7	1
Cobbler	46.5	4	66.2	2
Craigs Bounty	0.9	4	17.7	4
Colorado 6316	21.8	3	28.9	2
Colorado 6320	21.0	3	36.8	2
Colorado 6330	32.0	3	28.5	1
Colorado 6344	11.4	4	18.3	4
De Sota	39.2	4		
Early Gem	46.3	4	64.2	2
Earlaine	39.7	2	33.2	1
Empire	2.3	4	7.8	4
Erie	46.6			
Epicure	60.9	1	81.7	1
Essex	20.6	3		
Fillmore	8.7	3	8.7	1
Friso	0.6	3	11.8	2
Furore	5.8	4	6.0	4
Flava	25.5	2	91.7	1
Golden	10.0	2		
Green Mountain	12.5	4	29.2	2
Great Scott	5.8	4	34.1	3
Harford	2.5	2	3.3	1
Hindenburg	6.8	2	45.0	1
Houma	21.2	3	51.2	3
Iduna	2.8	4	8.7	3
Jubel	0.9	3	17.0	2
Katahdin	5.0	4	18.0	2
Kennebec	31.8	4	41.6	2
La Salle	41.0	3	55.0	1
Menominee	2.2	4	5.9	4
Marygold	31.3	1		
Mesaba	37.0	1		
Mohawk	7.8	4	23.0	3
Ontario	6.6	4	39.3	1
Placid	17.0	2		
Pontiac	30.2	2	42.8	2
Populair	3.3	4	0.7	4
Potomac	0.4	4	1.0	2
Progress	37.3	3	77.3	1
Rheingold	5.9	3	44.3	1
Record	8.2	2	28.3	1
Red Warba	57.1	4	78.7	2
Russet Burbank	25.9	4	69.4	4
Russet Rural	4.0	2	12.0	1
Saranac	0.3	4	2.7	4
Sebago	11.0	2	23.7	2
Sequoia	2.2	4	3.0	4
Skerry Champion	2.4	2	15.4	2
Starkeregis	11.5	2	24.2	2
Saskia	60.9	2	81.7	2
Teton	22.7	4	37.4	3
Triumf	10.2	4	32.0	2
Triumph	70.6	3	75.0	1
Wilpo	1.3	4	6.8	4
White Rose	33.1	4	51.3	3
Yampa	6.6	4	29.9	2

quate crop of tubers because of the very late appearance of the disease. Resistance in the extremely late varieties could not be accurately determined even during the long growing season in 1950. Varieties like Potomac, Populair, A.C. 25680 and Wilpo, which appeared to be the most resistant were so late in their growth habits that it could not be estimated whether resistance was within the plant or lateness afforded an escape from the disease. When little or no vascular browning could be found in the stems at the ground level, such varieties were believed to be resistant.

Varieties similar to Menominee appeared to have internal resistance as well as resistance due to lateness. Some Menominee plants had infection in the roots and showed minor leaf symptoms by late July, at the time symptoms were becoming noticeable in the susceptible Russet Burbank. Such infected Menominee plants, however, displayed only a few yellow leaflets on one-half of the lower leaves on one side of the plant. The yellowed leaflets later died and were retained on the plant in a dried condition without the remainder of the plant being visibly affected for more than 30 days. Only late in the growing season would such plants show progressive yellowing and death of the leaves throughout the plant. In Russet Burbank and other susceptible varieties, early infection resulted in increasing yellowing and death of the plant so that most of the leaves were dead and dry within 30 days.

In moderately resistant varieties, of which Mohawk is an example, changes in environment sometimes affected resistance. For example, when the Russet Burbank was dead in late August, 1950, the irrigation water was withdrawn from the field in which the test plot was located at Rexburg. As a result, the symptoms advanced rapidly in Mohawk and Cayuga, as well as in the more susceptible varieties, while the more resistant varieties, Menominee, Populair, Sequoia and 41956, showed no deleterious effect and continued without symptoms after water was restored. As a result, artificially produced drought was used thereafter as a means of determining resistance at Aberdeen. Irrigation water was withdrawn after August 15 each year to help magnify the effects of the disease upon previously infected plants.

An excess of water during the growing season also tended to intensify the symptoms on certain moderately resistant sorts and on susceptible varieties. Russet Burbank succumbed more readily in the low, wet portions of the field. Low spots in the experimental trials resulted in earlier and more severe symptoms in moderately or even highly resistant types than was found under the more nearly optimum conditions in other parts of the field. While the resistance of Menominee and 41956 was not broken down by excess water, slightly earlier and more severe symptoms were found under extremely wet conditions.

Nielsen (7) stated that Sebago, Menominee, and U.S.D.A. Seedling 47105 appeared to have resistance to Verticillium wilt

under field conditions in Idaho. Ayers (1), working at Prince Edward Island, Canada, pointed out that all the varieties he tested except Houma and Seedling F4328 showed moderate to high susceptibility. Included in the susceptible varieties were Sebago, Irish Cobbler, Green Mountain, Katahdin, Chippewa, Kennebec, and Pontiac. Cunningham (3) in New Zealand found four varieties resistant to Verticillium wilt but did not name them. The results of Nielsen and Ayers disagree on the Sebago variety, it being listed as resistant in Idaho and susceptible in Prince Edward Island. While different strains of Verticillium probably occur, these differences possibly can be explained on the basis of location and the severity of the disease development under different growing conditions. Sebago, grown at Aberdeen had an average disease index of 11.0 and could be classed as resistant (Table 6) but when grown at Rexburg under more severe conditions, it had an index reading of 23.7, which placed it in the moderately susceptible group. Houma, which Ayers lists as resistant, proved rather susceptible at Aberdeen, and Rexburg, Idaho, with respective index readings of 21.2 and 51.2.

As a result of 4 years of testing of named and numbered varieties at 2 locations in Idaho, the more highly resistant to Verticillium wilt in the field were found to be 41956, A.C. 25669, A.C. 25673, A.C. 25680, Empire, Harford, Iduna, Menominee, Populair, Potomac, Saranac, Sequoia ,and Wilpo. Most of the highly resistant varieties were late to extremely late in their growth habits. For this reason, 41956, which more closely resembles the medium-maturing lines, was considered to be outstanding in its resistance.

BREEDING FOR RESISTANCE

Following the first season of field testing, crosses were made between the more resistant varieties and types found in the field. Subsequent crosses were made with Russet Burbank as a female parent (5) and Early Gem as either a male or a female parent to introduce the russet skin character. Crosses were also made between early-maturing types which were generally susceptible and late sorts which appeared to have field resistance. Menominee, Populair, Saranac, Sequoia, Wilpa, A.C. 25669, A.C. 25680, and 41956 were frequently used as parents together with numbered seedlings which were genetically related to members of this group or were shown to be resistant in the field.

When the results of some of the crosses were tabulated, as in Table 7, it appeared that a high amount of resistance could be obtained even from two susceptible parents, since more than 40 percent of the progeny of family line A 102 were either healthy or only slightly infected. Of the progeny from crosses between resistant and susceptible parents, 50 to 70 percent were acceptable for resistance while resistant crossed with resistant yielded 70 to 100 percent of the progeny with an average index below

10. The maturity of the individual progeny, however, was not considered and the influence of lateness on resistance could not be determined. Physiological resistance as contrasted with genetic resistance could not be separated among the late-maturing types

Table 7.—Distribution of family lines for resistance to Verticillium wilt at Aberdeen.

Pedigree number	Parentage	Progeny with indicated Verticillium index					
		0-10	11-20	21-30	31-40	41-50	over 50
		Percent	Percent	Percent	Percent	Percent	Percent
Parents Both Susceptible:							
B2365	X1276-185 x B445-41		16.6	58.4	25.0		
A 102	Russet Burbank x Earlaine	40.6	14.8	11.1	22.2	7.4	3.7
Parents Resistant x Susceptible:							
A 101	Russet Burbank x Menominee	71.5	28.5				
B2913	X528-170 x B606-3	51.6	12.9	19.3	12.9	3.3	
Parents Both Resistant:							
B3019	Sequoia x B986-7	100.0					
A1	Menominee selfed	71.5	28.5				

Table 8.—Distribution of two family lines of similar parentage for maturity and disease symptoms at Rexburg.

Family line	Disease symptoms 110 days	Maturity of plants			Total
		Early	Medium	Late	
		Percent	Percent	Percent	Percent
A 116-Russet Burbank x Menominee (Medium-late susceptible x late resistant)	Severe	6.7	12.1	9.1	27.9
	Moderate	0.6	3.0	24.8	28.5
	Slight	0	0	37.0	37.0
	None	0	0	6.7	6.7
	Total	7.3	15.2	77.6	
A 124-Early Gem x Menominee (Early susceptible x late resistant)	Dead	21.2	6.1	1.0	28.3
	Severe	2.0	4.0	7.1	13.1
	Moderate	3.0	7.1	9.1	19.2
	Slight	1.0	1.0	16.2	20.2
	None	0	3.0	16.2	19.2
	Total	27.3	21.2	51.5	

in the relatively short growing season in Idaho. Mid-season maturity together with acceptable resistance would be necessary to determine whether a given line would make reliable parent material.

The segregation for maturity and disease of two family lines of similar parentage at Rexburg is shown in Table 8. Family line A116 is a cross of Russet Burbank x Menominee (a medium-late susceptible parent x a late resistant). To obtain family line A 124, Early Gem (Russet Burbank x X96-56), an early susceptible variety was crossed with Menominee.

When relatively late parents were used, as in the A116 line, over 75 percent of the progeny were late. While late susceptible plants were found, the majority of the progeny, 68.5 percent, were late and showed only moderate or less infection on September 2. In this cross there was little variation from the expected correlation between lateness and resistance in that no early or medium resistance was found. Among the late-maturing,

healthy, slightly or moderately affected seedlings, some were considered to have commercial possibilities although the value of such lines as parents for Verticillium-resistant plants was questionable.

In some crosses, when early parents were used with late resistant parents, of which line A124 is an example, a considerable break in the expected correlation was observed. While 51.5 percent of the seedlings were late and 43.5 showed no symptoms to moderate symptoms in the late class, 15 percent showed moderate or less symptoms in the early or medium class. Such seedlings were considered to be desirable for parent material.

From the crosses of russet-skin types with Verticillium-wilt-resistant lines and in certain of the backcrosses, more resistant russet type potatoes have evolved. Parent material of the russet type has been developed, many of the progeny are more fertile than the Russet Burbank or Early Gem and appear to carry a greater amount of resistance to Verticillium wilt. Several lines which do not have russet skins were found in crosses of resistant to resistant or to moderately resistant parents and have produced plants with a high type of resistance to Verticillium wilt in the field.

DISCUSSION

Verticillium wilt can generally be described as a disease of senesence in the potato plant since the symptoms in most varieties appear after blossoming and the cessation of rapid growth. The time of the appearance of the malady is varied by host resistance or by the lateness of the strain as well as by environmental variations. The rate of disease development is also influenced by climate, environment, resistance and lateness. The disease appears to develop sooner and more rapidly in plants on light sandy soils, on hillsides or in low, wet portions of the field. The conditions most conducive to severe Verticillium wilt are earliness of varieties, early planting, and first irrigations together with warm June temperatures followed by high temperatures in July and August. Conversely the conditions which bring about a delay in maturity such as cool temperatures and lateness of strains or varieties delay disease development.

Physiological resistance of susceptible host types is evidenced where the plant is kept in an actively growing phase over a longer period by the use of younger seed tubers and later maturing strains or where regrowth has been stimulated by removing the leaves or by other injury. Genetic resistance is found in some lines and is generally coincident with lateness although early- and medium-maturing sorts which are moderately to highly resistant under field conditions are appearing. The interaction of physiological and genetic resistance with the environment makes it possible to list a given variety as resistant under one set of conditions while it may prove moderately susceptible in a different

environment. Moderately resistant varieties similar to Mohawk and Sebago may be subjected to severe changes which break down such resistance relatively late in the growing season. Late maturity alone may provide sufficient resistance for the production of a maximum crop of tubers in relatively short growing seasons as is the case with Russet Rural grown at Aberdeen, Idaho.

Physiological resistance appears to be closely correlated with the time of tuber set. Stoloniferous types which set a few small tubers very late in the season show extreme resistance while those which set tubers early are generally very susceptible. Resistance seems to be more pronounced in the commercial-type selections in which tuber set is somewhat continuous as contrasted with a heavy early set of tubers.

The disease index, a weighted value based on the severity and progression of symptoms, is believed to be an adequate measure of the effects of the disease. Because of the highly significant correlation between increased disease symptoms and decreased yields in susceptible varieties at Rexburg, Verticillium wilt is considered to be the limiting factor in potato production on the Egin Bench.

Since Verticillium wilt in susceptible varieties can be greatly delayed, or even prevented (Tables 3 and 4), by the use of 6-month-old seed tubers, it is not inconceivable that susceptible varieties could be grown commercially in seriously affected areas if young seed produced elsewhere in the winter was used or possibly if growth-regulating chemicals were applied to the seed tubers or plants.

SUMMARY

Verticillium wilt of potatoes was believed to reduce the annual crop in Idaho by 20 percent with losses up to 50 percent on sandy and sub-irrigated soils. This disease was considered to be the limiting factor in potato production on the Egin Bench near Rexburg, Idaho, where the more serious losses occur.

Disease development was influenced not only by the variety but also by the environment and the age of the plant. Symptoms were delayed in young or actively growing plants but were increased by conditions which hastened maturity, such as earliness of variety, early planting, and early irrigation and high temperatures.

Verticillium wilt could be delayed or even prevented in susceptible varieties by the use of seed tubers which were 6 months from planting to planting as contrasted with the normal 12-month-old seed tubers. In some susceptible varieties the yield was increased by the use of the young seed stock.

The yield and size of the tubers on susceptible varieties were decreased in proportion to the earliness and severity of disease

development at Rexburg, Idaho. The susceptible Russet Burbank variety produced less than one third as large a yield of marketable tubers as did the most resistant varieties at Rexburg in 1952.

In testing 1200 different lines, which include more than 100 named varieties, many variations of resistance and susceptibility were found at two locations in Idaho. Physiological resistance was correlated with lateness of the type and in some instances provided sufficient resistance during a relatively short growing season. The moderate resistance found in the Mohawk and Sebago varieties could be broken down by severe changes in environment. Empire, Harford, Iduna, Menominee, Populair, Potomac, Saranac, Sequoia, Wilpo, A.C. 25669, A.C. 25673, and A.C. 25680 were found to be highly resistant late varieties. Because of the medium maturity habit and strong resistance found in 41956 it was considered to be outstanding in its resistance to Verticillium wilt.

Highly resistant progeny have been developed by using resistant parents in crosses. From certain crosses of early susceptible and late resistant parents, medium- and early-maturing resistant progeny were found. Types with a russet skin and adequate resistance to Verticillium wilt have been developed by crossing resistant parents with susceptible russet-type potatoes.

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